Intraspecific leaf functional trait variability of eight *Prosopis pallida* tree populations along a climatic gradient of the dry forests of northern Peru

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ABSTRACT

We studied intraspecific trait variability (ITV) in functional leaf traits of *Prosopis pallida* trees located in eight populations along a climatic gradient on the Peruvian coast. The objectives were (1) to determine the relative importance of ITV at different ecological scales; (2) to understand how functional leaf traits relate to each other, and (3) to know the main climatic factors related to ITV in *P. pallida*. We used the restricted maximum likelihood method to decompose the variance across three nested ecological scales (tree, plot, and population level). The relative variance decomposition showed that tree level was the main source of variation for leaf chemical composition and stomatal size and density, whereas the plot and population levels were the main sources of variation for gas exchange and structural variables, respectively. Leaf ITV followed the general trends of the *leaf economic spectrum*, with negative relationships of leaf mass per area with both photosynthetic rate and leaf nitrogen. Precipitation was not related to any of the leaf traits, while mean annual temperature was correlated negatively with leaf relative water content and positively with water use efficiency. Our results highlight the importance of ITV in *P. pallida* and the possible impact of climate change.

1. Introduction

The study of functional trait variation is useful to describe and understand plant physiology and community structure (de la Riva et al., 2015; Hulshof and Swenson, 2010; Volf et al., 2016). The causes of this variation could be interspecific and/or intraspecific, the latter being considered less important. However, recent studies indicate that intraspecific trait variability (ITV) can provide meaningful information about trait responses along environmental gradients (Laforest-Lapointe et al., 2014; Siefert et al., 2015), agricultural crop performance (Gagliardi et al., 2015; Okubo et al., 2012), and genetic selection (Arntz and Delph, 2001). ITV may explain how certain species can pass through both biotic and abiotic filters to maintain viable populations, promoting species coexistence (de la Riva et al., 2015; Jung et al., 2010; Messier et al., 2010).

ITV can be studied according to different levels of ecological scales: trees, plots, and populations, (Albert et al., 2010; Messier et al., 2010), which may provide different explanations of the causes of functional trait variability. At the population level, plant trait variation is affected by climatic factors such as temperature and precipitation (Fajardo and Piper, 2011; Richardson et al., 2013). In this sense, Albert et al. (2010)

found that 60% of the maximum height variation of *Dryas octopetala* L. was explained at the population level, and this variable had strong relationships with temperature and light radiation. Thus, high ITV at the population level may indicate that it arises from differences in climatic factors. However, other factors - such as soil texture, successional stage, and disturbance regimes - should not be ignored. The plot level, a subsample unit inside the population level, may also show trait variations and can provide information about the response to small-scale abiotic factors such as water and nutrient availability, soil compaction, and salinity. Plot-level variation may indicate factors limiting plant recruitment, the successional stage, and the ecological strategy of a species (Messier et al., 2010). On other hand, at the tree level, ITV may result from intra and/or interspecific site-competition for nutrients, light, or water (Albert et al., 2010; Messier et al., 2010; Schemske et al., 2009). High genetic variability within populations could also be responsible for variations at the tree level. However, genetic differences should be more relevant between populations, where gene flow may be reduced.

Studies of plant functional traits have already found that leaf structure (LMA, leaf dry mass per area) and leaf lifespan are negatively related to leaf physiology (A_{mass}, net photosynthetic rate per unit leaf

dry mass) and leaf chemical composition (LNC, leaf nitrogen concentration) (Poorter et al., 2009; Wright et al., 2004). These trade-offs between functional leaf traits represent the *leaf economic spectrum* (Wright et al., 2004), one extreme being represented by species with an *acquisitive resource strategy* (low LMA and high A_{mass}) and the opposite extreme by species showing a *conservative resource strategy* (Wright et al., 2004). At the intraspecific level, leaf traits may change among populations, the resource use strategy shifting to best suit the current environmental conditions. In this sense, Gagliardi et al. (2015) found that functional leaf traits in *Coffea arabica* covaried in patterns consistent with the *leaf economic spectrum*.

Previous works have studied ITV using experimental designs that included a wide study area with great changes in altitude and latitude (Fajardo and Piper, 2011; Hulshof and Swenson, 2010; Richardson et al., 2013). Both of these latter variables strongly influence temperature, irradiance, and several other environmental factors - such as soil texture and soil nutrient and water availability (Valladares et al., 2007). For example, the study of Fajardo and Piper (2011) covered an extensive area, with latitude from 36° to 46° south in Chile, with great differences in altitude and annual precipitation. Similarly, the work of Richardson et al. (2013) covered an area with latitude from 41° to 47° south in New Zealand, with large changes in altitude (from 0 to 1400 m a.s.l.), temperature and precipitation. Studies with many simultaneous stresses, strong environmental gradient intensity, and high genetic variability introduce strong ecological limits to phenotypic plasticity, hindering ITV (Albert, 2015; Valladares et al., 2007). Although these studies are interesting as they explore wide environmental gradients to understand the importance of environmental factors in ITV, covariation between climatic variables means that they overlap in their effects and influence one another, making it difficult to study them independently. Thus, experimental designs that avoid strong simultaneous stresses should also be considered.

The algarrobo (*Prosopis pallida* H. et Bonpl. ex Willd. H.B.K.), a leguminous tree adapted to long periods of drought, is a key species of the dry forests of the eastern coasts of Peru and Ecuador, and it represents approximately 61% of plant cover in the dry forests (Bravo et al., 2003). Because of its relevance in rural economy, most of the previous research about algarrobo has been focused on food applications (Grados et al., 2003; Liu et al., 2011). However, studies related to physiology and ecological characteristics are limited (but see Harris et al., 2003; Padrón and Navarro-Cerrillo, 2004) or they are focused on other species of this genera, such as: *P. alba, P. chilensis, P. juliflora, P. fleuxosa,* or *P. nigra* (Delatorre et al., 2008; López Lauenstein et al., 2012). Thus, ecological and physiological studies of *P. pallida* are needed to understand the importance of ITV in a climate change scenario.

In our case, we study the ITV in functional leaf traits of *P. pallida* in eight populations located in the dry forests of northern Peru. These eight populations follow a decreasing precipitation gradient and an increasing temperature gradient from east to west. These climatic factors have shown to have a significant impact on leaf traits, increasing the leaf dry mass per area and decreasing the leaf nitrogen concentration in hotter and drier conditions (Moles et al., 2014). Thus, these effects can change the relationships between these variables and other related leaf traits. In our environmental gradient, there is no significant change in altitude (15–232 m a.s.l.), latitude (5-6° south), or soil texture (sand fraction over 64% in all locations). Thus, no changes in atmospheric pressure, oxygen concentration, or temperature are found due to the altitudinal differences. Therefore, we expected that ITV may respond clearly and independently to variation in temperature and/or precipitation along the environmental gradient. The hypothesis underpinning this study is that it is possible to identify changes in the ITV of *P. pallida* at different spatial scales (tree, plot, and population) and that ITV at the population level could be related to the climatic variation from the coast to the foothills of the Andes in northern Peru.

We measured structural (LMA; LDMC, leaf dry matter content; stomatal size and density), physiological (A_{mass}, net photosynthetic rate

per unit leaf dry mass; g_s, stomatal conductance; LRWC, leaf relative water content), and chemical (C and N concentrations) leaf traits. Considering the severe water limitation in dry forests, structural and functional traits related to water exchange - such as stomatal density, stomatal size, and LRWC - were also included. These variables have been related to physiological traits like transpiration and photosynthetic rate (Wu et al., 2014); structural traits like LMA (Meziane and Shipley, 2001); and survival under water limitation and salinity (Orsini et al., 2012; Sun et al., 2014).

The general objective of this study was to assess the differential response of the ITV of *P. pallida* along a climatic gradient of precipitation and temperature in the dry forest of northern Peru. The specific objectives were (1) to determine the relative importance of the source of variation of ITV at different ecological scales (tree, plot, or population level); (2) to know if, at the intraspecific level, leaf traits relationships follow the *leaf economic spectrum* generally described for interspecific studies; and (3) to understand how functional traits at the population scale are related to environmental factors such as temperature and/or precipitation. These results will give us information about the importance of intraspecific variability and the possible impact of climate change in the *P. pallida* dry forest.

2. Materials and methods

2.1. Study sites

The *P. pallida* dry forests studied are located at 4°5′ – 6°22′ S and 79°00′ – 81°7′ W in the Piura province of north-western Peru, South America (hereafter abbreviated as Piura) (Fig. 1). The mean annual precipitation is between 48 mm and 354 mm, with moderately mild mean annual temperatures of 23.2–24.8 °C, and the altitude ranges from 15 to 232 m a.s.l (Rollenbeck et al., 2015). The dominant soils result from aeolian or alluvial deposition and the topography is characterized by semi-desert plains (Bravo et al., 2003). The study area consists mainly of forests, in which the principal species is *P. pallida*, accompanied by *Loxopterygium huasango* Spruce ex Engl. (hualtaco), *Bursera graveolens* (Kunth) Triana and Planch. (palo santo), and *Capparis angulata* R. & P. (sapote) in the tree stratum.

Unlike most tropical regions, the climatic conditions in this area are characterized by a lack of precipitation events and high climatic stability. Due to the thermal inertia of the Pacific Ocean, the sea surface temperature and air temperature are highly linked in this region and, because of the Humboldt current system and wind formations, are the main predictors of precipitation. Therefore, an increase in temperature is associated with higher precipitation, and a significant spatial variation exists across the region, from the coast to the foothills. A high temporal variation in weather conditions comes only from extreme precipitation events, related to a rise in temperature during the El Niño Southern Oscillation (ENSO). However, this event only appears every ∼7 years, and the rest of the time this region faces highly stable climatic conditions. Rollenbeck et al. (2015) found that during no-ENSO years the temperature follows a regular annual cycle and that it can be closely fitted with a sine wave with a phase length of one year and an amplitude of 7–9 °C.

2.2. Sampling design and data collection

Seven algarrobo populations, ranging from the coast to foothills, were selected to cover a variation in temperature and precipitation (Table 1, Fig. 1). Since one of them (Ñapique) presented high site variability related to the close proximity to a lake, we considered two different populations (Ñapique Wet and Ñapique Dry, the former being closer to the lake). Therefore, we considered a total of eight populations. Data sampling was carried out during a no-ENSO year (2014). Thus, the climatic conditions were stable. The mean annual temperature and precipitation for the 1950–2000 period for each site were obtained from the WorldClim -
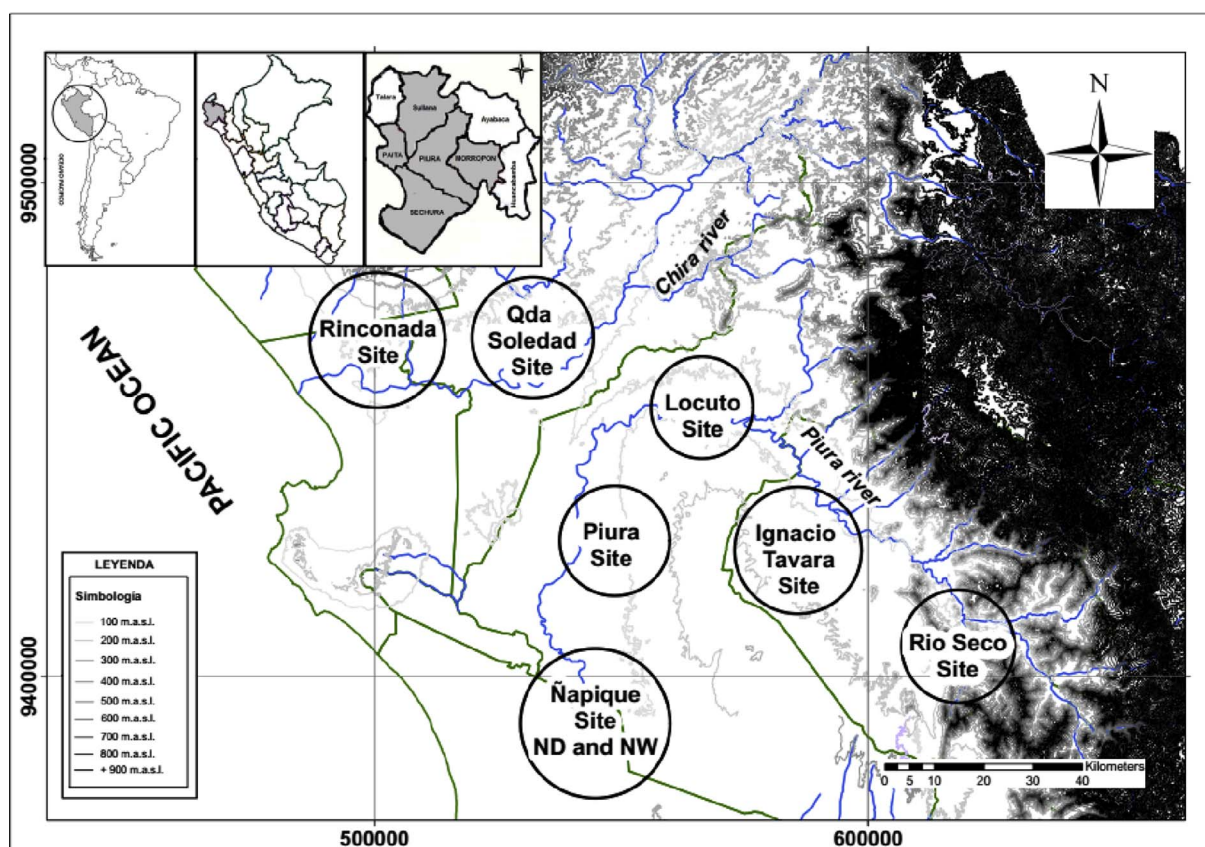
Fig. 1. Localization of the eight *Prosopis pallida* populations included in this study.

Table 1

Climate description and location (UTM) of the studied zones in northern Peru. Data obtained from WorldClim-Global Climate (Hijmans et al., 2005) for the period 1950–2000. MAP: Mean annual precipitation, MAT: Mean annual temperature. Zones were ordered according to altitude.

Zone name	Zone Code	MAP (mm)	MAT (°C)	Altitude (m a.s.l.)	Longitude	Latitude
Ñapique Wet	NW	81	23.7	15	17 M 533068	9,388,956
Ñapique Dry	ND	81	23.7	15	17 M 533068	9,388,956
Quebrada Soledad	QS	73	23.9	61	17 M 519339	9,455,070
Piura	PI	48	23.9	73	17 M 532471	9,433,785
Locuto	LO	157	24.3	69	17 M 568326	9,453,687
Rinconada	RI	52	23.4	97	17 M 498171	9,457,866
Ignacio Távara	TA	208	24.8	153	17 M 577205	9,433,091
Río Seco	RS	354	23.2	232	17 M 617468	9,415,078

Global Climate data (Hijmans et al., 2005). To know if the mean environmental data obtained from WorldClim were representative of the environmental conditions of the year of sampling (2014), we used the Climate Research Unit (CRU) database (https://crudata.uea.ac.uk/cru/data/hrg/cru_ts_4.00/ge/) to obtain annual temperature and precipitation data from each location. These data were obtained from extrapolation of the few climate stations located in the region. We correlated the CRU data of 2014 (the year of sampling) and WorldClim data and proved that the two data sources were strongly correlated (Appendix Fig. A1). Thus, we are confident that the environmental data represent the climate variations during no-ENSO years.

To cover all the spatial and microclimatic variability, three plots of 10 000 m^2 were chosen, considering similar tree density, the presence or absence of other species, and the edge effect within each site. The distance between plots ranged from 300 to 4000 m, to avoid pseudo replication. The soils in all plots and sites had a sandy texture (98%

sand), except Río Seco (RS) with a loam-sandy texture (29% silt and 7% clay). Within each plot, a random sampling inventory was developed and five adult trees of *P. pallida*, with a basal stem diameter exceeding 10 cm, were selected as experimental units for all plant measurements. Individual tree locations were recorded with a real-time differential global positioning system (GPSMAP 76CSx - Garmin USA International, Inc; Estimated Position Error < 1 m).

All the leaf traits measurements were taken in summer (between January and March), which is the growing season of *P. pallida* due to the rainfall episodes and temperature conditions. For physiological measurements (see below), three mature sun-exposed leaves with no signs of damage were randomly selected in each tree. The chosen leaves were located at a tree height between 1.5 and 2.5 m to facilitate data acquisition. Net photosynthetic rate (µmol CO_2 m^{-2} s^{-1}), transpiration rate (E; mmol H_2O m^{-2} s^{-1}), and stomatal conductance (g_s; mmol H_2O m^{-2} s^{-1}) were measured using an infrared gas analyzer (CID-Bioscience Inc, model CI-340). The measurements were made between 8:00 and 13:00 h (local time) on cloudless days, to achieve a mean (± SD) photosynthetically active radiation of 1279 ± 29 µmol m^{-2} s^{-1}. The average temperature during measurements was 37.6 ± 3.7 °C. The net photosynthetic rate per unit leaf area was converted to net photosynthetic rate per leaf dry mass (A_{mass}; nmol g^{-1} s^{-1}) using the individual leaf dry mass per area (g m^{-2}) (see methods below). The water use efficiency (WUE, nmol CO_2/mmol H_2O) was calculated as the ratio of the net photosynthetic rate to stomatal conductance (Quero et al., 2006). Some data were discarded due to the fact that measurements were made too early in the morning when the photosynthetic radiation was very low. Therefore, in some cases the mean data of individual trees for these physiological traits were calculated using between 10 and 15 measurements.

Additionally, in each tree a fully expanded, sun exposed branch was selected and mature leaves with no signs of damage were collected in hermetic bags and transported to the laboratory to obtain the leaf area

and dry mass. The leaves (including petiole) were scanned and leaf area was calculated using Image-Pro plus 4.5.0.29 software (Media Cybernetics, MD, USA). Leaf dry mass was measured, after drying the leaves at 80 °C for 24 h, using an analytical balance. Leaf dry mass per area (LMA) was calculated as the ratio of leaf dry mass to leaf area. A subsample of leaves from each tree was taken to analyze the carbon (LCC, %) and nitrogen (LNC, %) concentrations. For that, leaves were ground with a stainless steel mill and the C and N concentrations were measured using an elemental analyzer (Eurovector EA 3000; EuroVector SpA, Milan, Italy).

A subsample of fresh leaves was selected and taken in hermetic containers (previously weighed) to calculate the leaf relative water content (LRWC). In the laboratory, the containers were weighed and the leaves were taken to full water saturation and weighed again 10 h later. Finally, the leaves were dried at 80 °C for 24 h and weighed again. The LRWC was calculated using the following equation (Bussotti and Pollastrini, 2015): LRWC = (Fresh leaf mass - Dry leaf mass) × 100/ (Fully water-saturated leaf mass - Dry leaf mass). The leaf dry matter content (LDMC) was calculated using the following equation: LDMC = (Dry leaf mass/Fully water-saturated leaf mass) × 100.

To measure stomatal size and stomatal density, imprints of the leaf adaxial and abaxial surfaces were taken from a subsample of leaves using clear nail polish (Sampson, 1961). After five minutes, the imprints were taken using a transparent tape and then examined with a light microscope (Zeiss model Axioskop, Germany). Digital pictures of all imprints were taken, calibrated using a calibration slide micrometer, and analyzed using Adobe Photoshop 3CS (Adobe Systems). Stomatal density was calculated as the number of stomata (adaxial and abaxial surfaces) per unit area. In about ten stomata per leaf, we measured the long and short axis of each stoma, to calculate a proxy of stomatal area using the ellipse equation.

2.3. Statistical analysis

Prior to statistical analysis, all data taken from the same tree were averaged to use as a statistical unit. We examined the fit of all variables to the assumptions of normality and homogeneity of variance, using the Kolmogorov–Smirnov and Levene test, respectively. When the data did not fit a normal distribution, they were normalized by $\log_{10}$ transformations. Once the basic requirements had been met, structural and physiological variables were analyzed statistically using a nested analysis of variance (ANOVA) with the aov function of R (nesting the tree inside the plot and this inside the population) (R Development Core Team, 2007 version 3.2.2). When the studied variables showed significant differences at the population level, Tukey's test was used to detect differences between populations (Sokal and Rohlf, 1995). Then, we calculated the percentage of variance explained by the tree, plot, and population levels, following Messier et al. (2010). For that, we fitted a general linear model to the variance across the three scales nested one into another (i.e. nested ANOVA with random effects) in this increasing order: tree, plot, and population, using a restricted maximum likelihood (REML) method in the lme function of the "nlme" package of R.

To explore the relationships between leaf traits, Pearson's correlation analyses between physiological and structural traits at the tree level were performed. Multivariate relationships among the variables were studied using a Principal Component Analysis (PCA), to determine the variables that explained most of the variation. For the PCA, all leaf traits measured were included except E (highly correlated with g_s) and the adaxial stomatal area (highly correlated with the abaxial stomatal area). To study the effect of climatic factors on leaf traits, we used the mean data from every population and performed Pearson's correlation analyses between leaf traits and climatic factors (mean annual temperature, MAT; and mean annual precipitation, MAP). Also, correlations between the PCA axes and climatic factors were made. The Pearson's correlation analyses and PCA were performed using STATISTICA v8.0 (StatSoft, Inc. 2007).

Table 2
Mean ± standard error (n = 10–15) of leaf traits of *Prosopis pallida* populations in northern Peru (Piura Region). LMA: leaf dry mass per area; LDMC: leaf dry matter content; LRWC: leaf relative water content; A_mass: net photosynthetic rate per leaf dry mass; g_s: stomatal conductance; WUE: water use efficiency; LCC: leaf carbon concentration; LNC: leaf nitrogen concentration; stomatal density (number of stomata per mm²). Different letters indicate significant differences between populations at P ≤ 0.05 (One way ANOVA; Tukey test). The coefficient of variation (CV) within each population is shown. The significance of Population (Pop) and Plot are shown as NS, non-significant; **P** < 0.01; ***P** < 0.001.

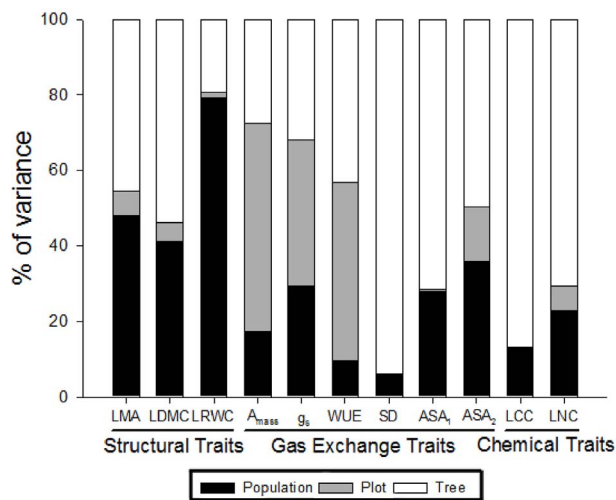| Zone Code	LMA (g m⁻²)	LDMC (%)	LRWC (%)	A_mass (nmol CO₂ g⁻¹ s⁻¹)	g_s (mmol H₂O m⁻² s⁻¹)	WUE (nmol CO₂ mmol H₂O⁻¹)	Stomatal density (# per mm²)	Abaxial stomatal area (µm²)	Adaxial stomatal area (µm²)	LNC (%)	LCC (%)
NW	85.4 ± 3.36^{ab}	28.0 ± 0.84^{ab}	85.4 ± 2.1^{a}	77.3 ± 8^{ab}	28.8 ± 2.8^{a}	0.245 ± 0.03^{bc}	1229 ± 53	84.1 ± 10.2^{a}	85.8 ± 8.4^{a}	3.15 ± 0.08^{c}	44.21 ± 0.5^{ab}
ND	87.9 ± 2.9^{ab}	27.8 ± 0.64^{ab}	75.9 ± 2.1^{b}	47.0 ± 9.1^{bc}	15.9 ± 1.8^{b}	0.254 ± 0.04^{abc}	1462 ± 152	70.1 ± 11.2^{ab}	59.7 ± 3.8^{ab}	3.54 ± 0.09^{b}	45.72 ± 0.3^{a}
QS	97.5 ± 3.63^{a}	33.4 ± 0.91^{a}	56.7 ± 1.1^{c}	75.6 ± 10.8^{ab}	29.2 ± 5^{a}	0.289 ± 0.02^{ab}	1870 ± 184	51.6 ± 5.7^{abc}	46.1 ± 3.7^{bc}	3.40 ± 0.11^{bc}	43.93 ± 0.4^{ab}
PI	66.1 ± 2.67^{cd}	23.5 ± 0.9^{b}	75.6 ± 2.2^{b}	99.4 ± 17.4^{ab}	25.0 ± 3.68^{ab}	0.251 ± 0.01^{abc}	1656 ± 163	54.7 ± 6.3^{abc}	46.8 ± 8.4^{bc}	3.69 ± 0.15^{ab}	43.89 ± 0.3^{b}
LO	65.1 ± 3.61^{d}	25.1 ± 1.35^{b}	74.1 ± 2.2^{b}	107.2 ± 9.2^{a}	29.2 ± 2.4^{a}	0.259 ± 0.02^{abc}	1781 ± 268	40.4 ± 4.0^{c}	38.6 ± 3.5^{c}	4.21 ± 0.13^{a}	44.14 ± 0.5^{ab}
RI	64.1 ± 4.14^{d}	24.4 ± 0.93^{b}	86.4 ± 1.8^{a}	85.4 ± 15.0^{ab}	23.5 ± 2.9^{ab}	0.202 ± 0.02^{c}	1316 ± 121	59.2 ± 6.2^{abc}	47.0 ± 5.1^{bc}	3.75 ± 0.19^{ab}	43.6 ± 0.2^{b}
TA	94.7 ± 2.96^{a}	33.2 ± 0.45^{a}	51.6 ± 1.3^{c}	32.7 ± 6.9^{c}	9.5 ± 1.9^{c}	0.336 ± 0.02^{a}	1387 ± 128	47.9 ± 5.0^{bc}	43.3 ± 2.9^{bc}	3.24 ± 0.13^{bc}	43.86 ± 0.4^{b}
RS	78.7 ± 3.54^{bc}	27.9 ± 1.76^{ab}	89.8 ± 1.5^{a}	59.4 ± 11.0^{abc}	23.0 ± 4.3^{ab}	0.188 ± 0.02^{c}	1520 ± 128	81.1 ± 7.2^{a}	79.2 ± 5.5^{a}	3.69 ± 0.16^{ab}	44.87 ± 0.2^{ab}
CV (%)	22.5	18.5	19.9	57.8	51.4	31.7	35	43.3	40.3	16.8	3.5
Pop	***	***	***	***	***	***	NS	***	***	***	**
Plot	NS	NS	NS	***	**	**	NS	NS	NS	NS	NS

Fig. 2. Source of variation within variables. Relative variance decomposition at the tree (white bar), plot (gray bar), and population (dark bar) levels for LMA: leaf dry mass per area; LDMC: leaf dry matter content; LRWC: leaf relative water content; A_{mass}: net photosynthetic rate per leaf dry mass; g_s: stomatal conductance; WUE: water use efficiency; SD: stomatal density; ASA1: abaxial stomatal area; ASA2: adaxial stomatal area; LCC: leaf carbon concentration; and LNC: leaf nitrogen concentration.

3. Results

3.1. Sources of intraspecific leaf traits variability

All the leaf traits studied differed statistically among the eight populations, except for stomatal density (Table 2). Structural leaf traits (such as LMA and LDMC) had their highest values in Ignacio Távara and Quebrada Soledad, two of the sites with higher mean annual temperature. The Ignacio Távara population had also the lowest LRWC, A_{mass}, and g_s (Table 2). Despite the significant variability of the leaf chemistry traits among populations, LCC and LNC had the lowest

coefficients of variation among all the traits (3.4 and 16.7, respectively). In the case of the two Ñapique populations, we expected to find large differences in leaf traits related to the proximity to a lake. However, in general, we did not find significant differences between these two populations, although Ñapique Wet, the population closest to the lake, had a higher mean value for LRWC and g_s and a lower LNC.

The population factor explained a high percentage of the variance (40–80%) of the structural leaf traits (such as LMA, LDMC, and LRWC) (Fig. 2). The plot level accounted for a significant amount of the variance in the gas exchange variables (e.g. A_{mass}, g_s, and WUE) (Fig. 2). Variables related to stomatal variation (stomatal density and stomatal size), leaf chemistry (LCC and LNC), and leaf structure (LMA and LDMC) were explained to a high degree (> 50%) at the tree level (Table 2, Fig. 2).

3.2. Leaf traits relationships

The LMA was negatively correlated with A_{mass} and LNC (Fig. 3A and B), following the trend of the *leaf economic spectrum* (Appendix, Fig. A2), and positively with LDMC (Appendix, Table A1). The LRWC was negatively correlated with LDMC and WUE (Fig. 3C and D).

The PCA was used to reduce multivariate variation and determine which variables explained most of the variation in leaf traits. The first axis of the PCA (accounting for 28% of the variance) was correlated positively with LMA and LDMC and negatively with gas exchange variables (A_{mass} and g_s) (Fig. 4). This axis corresponded in the positive side with most of the trees studied in Ignacio Távara and Quebrada Soledad, the populations with higher mean annual temperature, and in the negative side with the Locuto and Piura populations. The second axis of the PCA (explaining 17% of the variance) was mainly related to the increase in LRWC and stomatal area, and to the decrease in WUE and stomatal density (Fig. 4). As expected, the gas exchange variables (A_{mass} and g_s) were positively correlated with each other, as were the adaxial and abaxial stomatal areas (Appendix, Table A1).
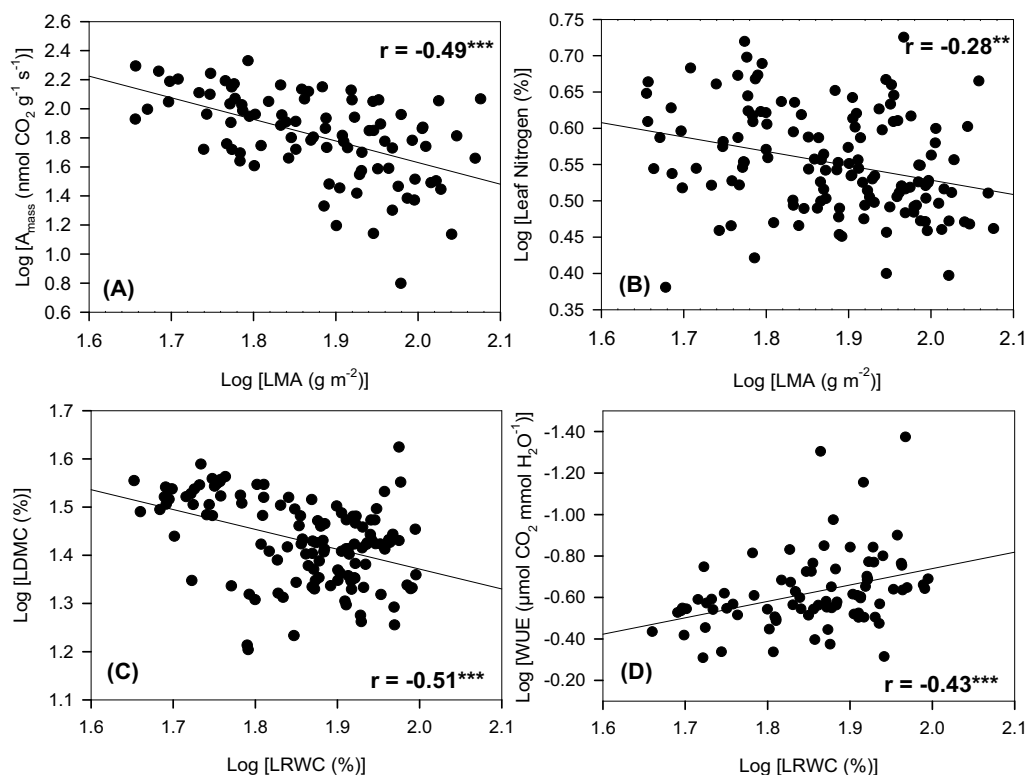

Fig. 3. Bivariate trait correlations at the tree level. Relationship of leaf dry mass per area (LMA) with (**A**) net photosynthetic rate per leaf dry mass (A_{mass}) and (**B**) leaf nitrogen concentration. Relationships of leaf relative water content (LRWC) with (**C**) leaf dry matter content (LDMC), and (**D**) water use efficiency (WUE). The correlation coefficient (r) and the significance are shown. $*P < 0.05$; $***P < 0.001$.
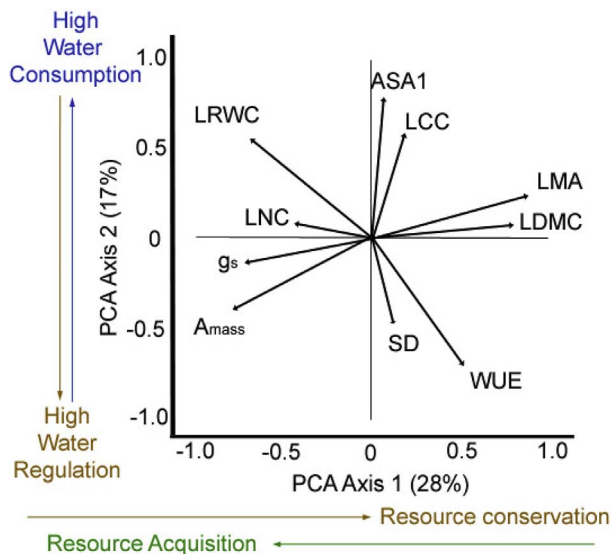
Fig. 4. Principal component analysis (PCA) to determine the multivariate relationships among leaf traits: abaxial stomatal area (ASA1), leaf carbon concentration (LCC), leaf dry matter content (LDMC), leaf dry mass per area (LMA), leaf nitrogen concentration (LNC), leaf relative water content (LRWC), net photosynthetic rate per leaf dry mass (A_{mass}), stomatal conductance (g_s), stomatal density (SD), and water use efficiency (WUE).

3.3. Relationships between leaf traits and environmental factors

At the population level, the mean leaf traits did not show any relationship with mean annual precipitation (Table 3). However, mean annual temperature was correlated negatively with LRWC and abaxial stomatal area, and positively with WUE (Table 3). Thus, mean annual temperature was positively related to the main axis 2 of the PCA, which is controlled by water regulation traits (Fig. 5). Gas exchange variables were not correlated with mean annual temperature or precipitation (Table 3).

4. Discussion

We found high trait variability among the eight *P. pallida* populations of the dry forests along a climatic gradient in northern Peru. Structural (LMA) and gas exchange (A_{mass}) traits were highly variable comparable to trait variation in the *leaf economic spectrum*; however, this was not the case for the leaf chemical composition (Appendix Fig. A2). The tree, plot, and population levels explained the variation of different leaf traits at differing extents. At the tree level, functional intraspecific leaf trait variations followed the general trends of the *leaf economic spectrum*, described, in general, at the interspecific level. At the population level, the variation in functional traits did not follow the precipitation gradient, but showed a significant relationship between water regulation variables and mean annual temperature.

4.1. Sources of intraspecific trait variability

Variations of leaf functional traits differed between distinct ecological scales. Differences in the variance explained by the population, plot, and tree levels allow us to understand which one of these scales
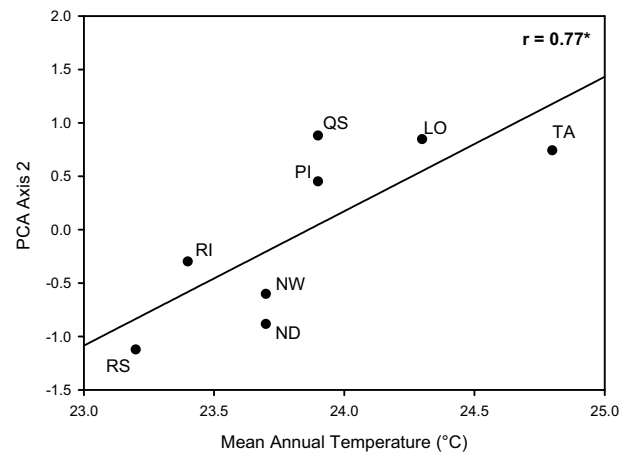

Fig. 5. Relationship of mean annual temperature with Axis 2 of the PCA at the population level. $*P < 0.05$.

contributes the most to the traits variation. At the population level, ITV is generally affected by both external conditions - such as climatic factors, disturbance regime, or soil fertility - and internal conditions, such as succession stages, plant phenology, or ontogeny (Kazakou et al., 2009; Messier et al., 2010). In our case, LRWC, LMA and LDMC showed a high amount of variation explained at the population level. The latter two variables are associated strongly with plant strategies, and are mostly known to be associated with climatic factors (Moles et al., 2014; Wright et al., 2005). Arid and semiarid ecosystems tend to have high-LMA leaves, which might be an adaptation to protect leaf function under dry conditions (Niinemets, 2001).

At the plot level, ITV may be due to local processes - such as the edaphic, hydric, and topographic conditions. Results for variance partitioning commonly show a small percentage at this level (Albert et al., 2010; Messier et al., 2010); however, it depends on the plot variability. In our case, the variability of gas exchange traits (A_{mass}, g_s, and WUE) was mainly explained at the plot level (Fig. 2). Similarly, in *P. juliflora*, gas exchange traits were limited by high solar radiation, which can change according to the population, position of plot (edge effect), or degree of herbivory (Elfadl and Luukkanen, 2006).

At the tree level, ITV may be due to relatively small-scale factors like air humidity, wind, resource availability, radiation regime, and genetic variation (Messier et al., 2010). In our study, a high amount of variance was explained at the tree level for chemical composition traits (LCC and LNC), stomatal variables (stomatal density and stomatal size), and structural traits (LMA and LDMC). Differences in LNC may indicate differences in soil fertility, resource availability, or degree of root development among trees (Guevara et al., 2010; Luo et al., 2016; Siefert et al., 2015). However, considering that LNC and LCC had the lowest coefficients of variation among all the traits and that most of this variation was at the tree level, we may assume that the variation comes from intrinsic factors such as root development and not from extrinsic factors like soil fertility or water availability (Decuyper et al., 2016). Of all the leaf traits, LMA is arguably the most studied, and represents the link between leaf structure and function (Poorter et al., 2009; Siefert et al., 2015; Wright et al., 2004). Almost half of the variance in LMA was explained at the tree level, and similar results (52%) have been found for *Nothofagus* sp. in New Zealand across environmental

Table 3
Pearson correlation coefficients between leaf traits of *P. pallida* and mean annual temperature (MAT) and precipitation (MAP) at the population level. $*P < 0.05$, $**P < 0.01$. For abbreviations see Table 2. Bold font means significant values.

	LMA	LDMC	LRWC	A_{mass}	g_s	WUE	Stomatal Density	Abaxial stomatal area	Adaxial stomatal area	LCC	LNC
MAT	0.28	0.41	**−0.82***	−0.17	−0.39	**0.91****	0.20	**−0.71***	−0.59	−0.32	−0.10
MAP	0.12	0.24	−0.10	−0.40	−0.27	0.16	−0.01	0.22	0.32	0.26	0.11

gradients (Fajardo and Piper, 2011), for many tropical species (48%) in Panama (Messier et al., 2010), and for perennial species (70%) in Belgium (Harzé et al., 2016). For LDMC, the variance percentage explained at the tree level was even higher (53%) than in other studies (Albert et al., 2010; Messier et al., 2010). This contrasts with recent studies indicating that leaf structure may be constrained around specific values within each species (Siefert et al., 2015). However, Harzé et al. (2016) showed that LMA and LDMC can be highly variable under different soil water conditions. While groundwater might be equally heterogeneous at the tree, plot, and population scales, we believe that root development could differ among trees. Decuyper et al. (2016) found differences in root growth at the tree and population levels. This suggests that limited root development has a detrimental effect in sites with less groundwater. Considering that *P. pallida* is a phreatic species with facultative deciduous leaves, it is possible that its leaf structure variability depends on the underground water supply.

4.2. Leaf trait relationships

The ITV at the tree level also provides basic information about phenotypic plasticity and how the variations in leaf traits are related to each other, to optimize plant performance. The LMA and LDMC are key leaf traits that describe leaf structure and leaf mass investment. They are highly correlated, and related to leaf lifespan, leaf chemical composition, and leaf gas exchange rate (Poorter et al., 2009; Wright et al., 2004). In our case, LMA and LDMC in one extreme and A_{mass} and g_s in the opposite extreme were the main drivers of variation in the first PCA axis. Similar results with A_{mass}, LNC, LMA, and LDMC have been found in coffee (Gagliardi et al., 2015) and *Nothofagus* sp. (Richardson et al., 2013), suggesting that leaf mass investment may be a decisive factor in leaf traits variations. The relationship between LMA and A_{mass} has long been studied in plant ecology (Donovan et al., 2011; Wright et al., 2004). There was no evidence of this relationship at the intraspecific level in *Prosopis* species (Vilela et al., 2003); however, ITV studies have found this type of relationship for other species (Gagliardi et al., 2015; Richardson et al., 2013). Comparing our results with the data of the *leaf economic spectrum* (Wright et al., 2004), we could consider *P. pallida* a resource acquisitive species with quick returns from leaf investments (Appendix, Fig. A2). This is supported by the high LNC, which was also negatively correlated with LMA.

The abaxial stomatal area (ASA1), LRWC, and water use efficiency (WUE) were the main drivers of variation in the second PCA axis, which showed a dichotomy between water consumption traits (ASA and LRWC) and water regulation traits (WUE and stomatal density). This is supported by the strong negative relationship of LRWC with both LDMC and WUE (Fig. 3C and D). In *P. juliflora*, stomatal control is quite sensitive to humidity and temperature, thereby regulating water loss and gas exchange (Elfadl and Luukkanen, 2006). This indicates that water control variables are associated with the optimization of gas exchange in *P. pallida*, which reduces water consumption and increases WUE when water availability is low.

4.3. Leaf trait response to climatic factors

Despite the high intraspecific leaf trait variability and the strong precipitation gradient across all the populations studied, there was no relationship between mean annual precipitation and any of the leaf traits studied. Similar results were found in *Prosopis alba* and *P. flexuosa*, where WUE was not affected by a decrease in water availability (Vilela et al., 2003; Villagra et al., 2005). Dryland ecosystems, and specifically dry forests in northern Peru, show a long period of drought over the year, with about seven months without rain (Appendix, Fig. A3). Moreover, this region receives extremely low annual rainfall (less than 300 mm); far lower than most *Prosopis* dryland forests (300–600 mm). Hence, its intensity and periodicity may explain why functional leaf traits variation does not relate to annual precipitation, at least during

no-ENSO years.

The lack of response to precipitation suggests that *P. pallida* has some compensatory physiological mechanism that counteracts leaf water loss - such as transpiration reduction, minimum photosynthetic rates, low water potential, and underground water uptake - even at high temperature (Delatorre et al., 2008). In fact, low water potential and high underground water availability in *Prosopis tamarugo* have been used to hypothesize a water movement cycle, where water flow from deep roots to the leaf during the day, and backward flow during the night to a root mat under the soil surface, allowing growth and production in dry conditions (Chávez et al., 2012; Garrido et al., 2016). This type of root morphology is common in *P. flexuosa* populations, where the water table is close to the surface (4–7 m depth) and provides a reliable way to grow and reproduce with less than 350 mm of mean annual precipitation (Guevara et al., 2010). According to our results and site characteristics, we could expect a similar water movement mechanism in *P. pallida* - at least in populations where high humidity benefits stomatal control, gas exchange (Elfadl and Luukkanen, 2006), and water flow through the roots.

It is worth noting that the inclusion of a population located close to a lake (Ñapique Wet) did not influence the lack of relationship between precipitation and functional traits. Ñapique Wet and Ñapique Dry showed similar mean values of all traits except LRWC, g_s, and LNC. Also, excluding NW from the correlation analysis did not change the main results. This also suggests that the underground water depth is not a decisive factor in functional trait variation, at least in this location.

Among the other environmental factors studied, mean annual temperature was highly correlated to the second PCA axis. In other studies, temperature has been the main source of variation and is also known to affect leaf mass investment variables such as LMA (Fajardo and Piper, 2011; Poorter et al., 2009), LDMC (Albert et al., 2010), and leaf thickness (Richardson et al., 2013). In *Prosopis* sp., variation in temperature has been found to affect leaf physiology and radial growth (Morales et al., 2001). Delatorre et al. (2008) found that temperature affects *Prosopis chilensis* in the same way as water deficit, reducing transpiration and the photosynthesis rate due to stomatal closure (Elfadl and Luukkanen, 2006). However, we did not find a relationship between mean annual temperature and A_{mass}, LMA, or g_s - probably because mean annual temperature variability was lower (23.2–24.8 °C) than in other studies and these traits only present significant variation under large changes of environmental factors (Messier et al., 2010). Despite that, we found a strong negative correlation of mean annual temperature with both LRWC and abaxial stomatal area; and a strong positive correlation with WUE. Moreover, these three variables, aside from leaf stomatal density, were the main drivers of variability in the second PCA axis, which explains why MAT was highly correlated with it. A significant increase in WUE has been considered a mechanism to cope with drought and arid conditions, favoring leaf water conservation (Arntz and Delph, 2001). This indicates that water regulation variables may play an important role in leaf physiology in *P. pallida*, even under small variations of mean temperature (± 2 °C). A relationship between stomatal control, gas exchange, and temperature has been found also in the genus *Prosopis* (Delatorre et al., 2008; Elfadl and Luukkanen, 2006), supporting our findings. In our case, there was a negative correlation between WUE and g_s (r = − 0.28, *P* < 0.05). Thus, the increase in water regulation seems to be controlled by stomatal closure and water flux through the leaf, without strongly affecting carbon flux through the leaf.

Due to the wind flow direction, Río Seco showed the highest MAP. However, due to the weakness of the wind flow at 150 km from the coast, warm breeze from the coast mix with cold breeze from the mountain and reduce air temperature in RS. Thus, it also showed the lowest MAT in the region. This allows us to study the effect of high water availability without the stress that comes from high temperature. Our results show that while precipitation has a higher variation along the climatic gradient its effect does not have the same significance as

the change in temperature. Therefore, water regulation traits seem to be restricted when temperature increases, even if precipitation increases, in this climatic gradient. However, excluding the Río Seco population there is a significant correlation between MAT and MAP, and therefore, we can not conclude that water regulation traits respond better to temperature than to precipitation. In this sense, Río Seco could be considered as an outlier in our dataset because it has also a soil texture less sandy that the other studied places and this could affect the relationships with water related traits. However, there are *Prosopis pallida* populations in places with environmental conditions similar to Río Seco (Mantaro Valley and Cajamarca, near the Andes Mountains), therefore Río Seco could not be strictly an outlier. In any case, similar populations of *Prosopis pallida* with less sandy soil and located near the Andes Mountains should be studied to reach an absolute corroboration of the differential effects of temperature and rainfall and confirm the trend between water regulation traits and MAT (Bravo et al., 2003).

However, excluding the RS population there is a significant correlation between MAT and MAP, and therefore, water regulation traits could respond to variation in both precipitation and temperature. Hence, similar populations with less sandy soil and located near the Andes Mountains should be studied to reach an absolute corroboration of the differential effects of temperature and precipitation and to confirm the trend of water regulation traits in response to MAT (Bravo et al., 2003).

Current IPCC reports estimate that precipitation will increase in the Niño 3.4 (5°N-5°S, 170°W-120°W) and Niño 1 + 2 (0°-10°S, 90°W-80°W) regions of the Pacific Ocean (including the north Peruvian coast) due to the increase in sea surface temperature (Bates et al., 2008). Our results suggest that the increase in temperature will have a highly detrimental effect on *P. pallida* populations, and the increase in precipitation might not be enough to compensate it. Moreover, theoretical considerations suggest that changes in precipitation, unlike temperature, are difficult to predict. This could explain why mean annual temperature in the area has been rising in the last decade without a significant increase in precipitation. Under these conditions, *P. pallida* populations would start to struggle, water loss through the leaf will increase stomatal closure, and, as a consequence, gas exchange will be reduced until hydraulic conductivity cannot be sustained (Bongers et al., 2017; Sevanto et al., 2014). Forest conservation will depend on the natural selection of resistance phenotypes if this trend is fully confirmed. Its high ITV at the tree level suggests that *P. pallida* has high genetic variability; however, survival of new seedlings depends heavily on ENSO events (Squeo et al., 2007). Therefore, the frequency and intensity of these extreme climatic events may determine the success and maintenance of the forest in the future.

5. Conclusions

Functional leaf traits of *Prosopis pallida* have shown high intraspecific variability. Relative variance decomposition shows that leaf structure is highly variable at the population level, while gas exchange variations are higher at the plot level and stomatal variation and leaf chemistry variations are higher at the tree level. The relationships between leaf traits followed the general pattern of the *leaf economic spectrum*, with one extreme showing a fast resource acquisition strategy (high-A_{mass} and low-LMA leaves) and the other extreme a conservative resource strategy (with the opposite traits). The leaf water economy also showed a dichotomy among individuals, with high-water-consumption leaves (at one end) having bigger stomata and high LRWC, and high-water-regulation leaves having high stomatal density and WUE. Mean annual temperature seems to play a more important role in the intraspecific variability of leaf traits than mean annual precipitation. However, further research along this gradient is required to confirm this trend. These results provide an insightful understanding of leaf trait adaptations in the dry forest and in a climate change scenario.

Appendix. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2018.01.010.

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